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Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*

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Studies attempting to document reproductive or other pre-lethal senescence effects in wild birds typically face an array of problems, including flaws in statistical analyses, non-adaptive philopatry to deteriorating environments, confounding effects arising from cohort heterogeneity and differential death rates of phenotypes and the frequent pairing of old birds to younger mates. Furthermore, recent studies suggest that birds could maintain a high level of physical fitness until old age, before being struck by a catastrophic illness leading quickly to their demise. The presence of terminally ill individuals in most datasets (and their greater incidence in older age categories) may therefore provide a false impression of progressive senescence in cross-sectional analyses. This study was designed explicitly to avoid all the known pitfalls linked to the demonstration of progressive senescence in wild populations, and involved one of the very longest-lived bird species. We show that, during incubation, old (aged 35 years and over) male grey-headed albatrosses *Thalassarche chrysostoma* make longer foraging trips, and have lower daily mass gains, than experienced mid-aged individuals (aged up to 28 years). This is, to our knowledge, the first report documenting reduced foraging performance with old age. Hatching and breeding success of pairs composed of two old individuals were reduced in comparison to mid-aged pairs. Overall results were very similar when analyses were repeated using only individuals known to have survived 1 or 2 years beyond field measurements (hence probably not suffering from the effects of an advanced terminal illness). We conclude that extremely long-lived individuals usually experience some degree of general physical deterioration, leading to reduced foraging and breeding performance, long before their final demise.

Keywords: foraging performance; life histories; age; breeding performance

1. INTRODUCTION

Senescence is a decline in physiological functioning with age that can lead to reduced survival and poor reproductive performance. The rate of aging in different organisms appears to be dictated by natural selection, resulting in considerable variability within groups of species with broadly similar anatomical and physiological characteristics, including metabolic rate (e.g. Ricklefs 1998; Finch & Austad 2001; Holmes *et al.* 2001). Birds are remarkably long-lived compared to mammals (e.g. Holmes & Austad 1995) and they therefore represent excellent models for research on the little-known mechanisms and evolution of retarded aging (Holmes *et al.* 2001).

Despite considerable technical difficulties (reviewed by Nisbet 2001), a considerable pool of studies has documented apparent actuarial senescence (increase in mortality rate associated with aging) in both short- and long-lived birds (Newton 1989; Newton & Rothery 1997; Holmes *et al.* 2001). Obtaining convincing evidence for other senescence effects (including changes in reproductive performance) in wild birds has proved much more difficult for several reasons. Success in breeding is usually determined by the combined efforts of both parents, for only one of which is the age known in many cases: therefore, as partnerships are not random, patterns are difficult to interpret. If pairs of old birds have an increased probability of break-up through the death of one individual, then (surviving) old birds might show reduced breeding output because of the failure to attract a new mate, the relatively short duration of successive pair-bonds, or the disadvantage of re-mating with inexperienced individuals (e.g. Bradley *et al.* 1990; Catry *et al.* 1997, 1998). Another confounding factor relates to potential non-adaptive breeding philopatry in changing environments resulting in deterioration of territory quality for old individuals (e.g. Rockwell *et al.* 1993). In addition, there may be negative phenotypic covariance between traits that favour reproduction and survival. If a species adopts a dual strategy, with some individuals showing consistently low reproductive effort and high survival, and others a high effort and low survival, then the predominance of low-effort birds among the older living cohorts could result, in a cross-sectional analysis, in apparent progressive senescence in reproductive performance (Pugesek & Wood 1992; Nisbet 2001). Finally, many published studies also suffer from shortcomings in statistical analyses, because authors often wrongly assume that a significant negative quadratic effect of age on

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a fitness correlate (such as breeding success) implies a significant decline in that parameter in old age, and hence senescence (Newton & Rothery 1997). Very few studies have dealt satisfactorily with these issues.

Ricklefs (2000) (see also Ricklefs & Sheuerlein 2001) observed that the shape of the senescence curve (the age-related mortality component of the Weibull model, that he attributed to intrinsic causes) does not change in captive populations. This implies that increased mortality of old individuals in the wild has causes similar to those affecting birds in captivity. Because the negative effects of predators, weather and reduced foraging ability are largely eliminated in captivity, it was concluded that the age-related decline in survival reflected intrinsic deterioration leading directly to death, for example due to stroke, heart disease or cancer. It should be noted, however, that external factors such as infectious disease could still affect both captive and wild birds. As there is no evidence of increased vulnerability to external factors in nature, Ricklefs (2000) inferred that physical and physiological fitness remain high until the end of life. The implication of this is that reproductive senescence should be negligible, except perhaps late in life when an individual has developed a terminal illness.

Coulson & Fairweather (2001) reanalysed the data from the well-known long-term study on kittiwakes *Rissa tridactyla* in northeast England, to test whether patterns of reduced breeding output in old individuals were the result of progressive senescence, or arose from breeding failure of individuals suffering from an advanced illness on their terminal breeding attempt. They found that individuals performed poorly in their final breeding attempt, irrespective of age, and recorded no differences in performance between the penultimate and third from last season (Coulson & Fairweather 2001). These results support the terminal illness hypothesis, with the implication that birds remain physically fit until very close to their death.

Given the many potential methodological and analytical problems, the apparent lack of reproductive senescence in several studies (e.g. Nisbet *et al.* 2002) and the recent evidence suggesting that long-lived birds may remain physically fit until an advanced age, there is clearly a pressing need to conduct new studies assessing whether reproductive senescence and general physical deterioration affect old individuals in wild bird populations. It is in the longest-lived taxa that most individuals reach ages where senescence effects are apparent (Ricklefs 1998). Grey-headed albatrosses *Thalassarche chrysostoma* are amongst the very longest-lived birds. Only a handful of species are known to share the extreme life-history traits associated with such high longevity: unusually long deferral to first breeding (10–14 years), obligate biennial reproduction when breeding is successful and an adult annual survivorship typically greater than 96% (Prince *et al.* 1994). Studies of grey-headed albatrosses have not yet continued for long enough to document close to maximum longevity records; the oldest known-age individuals are now 46 years old, but it is quite likely that some individuals live considerably longer.

In this paper we test if, after taking into account all the possible difficulties and shortcomings inherent in similar previous analyses (as described earlier), grey-headed albatrosses show an age-related deterioration in reproductive function and foraging performance prior to their terminal breeding attempt. By concentrating on individual foraging performance, we avoided problems of linkage between variation in breeding success, pair-bond duration and the age and abilities of the partner, as well as potentially non-adaptive philopatry to deteriorating breeding sites.

Incubation is a critical phase in albatross breeding cycles; on average, 58% of breeding failures occur at this stage in the grey-headed albatross (Prince *et al.* 1994). During incubation, only one individual can forage at a time, as the egg needs to be permanently attended—otherwise it is immediately predated. Hence, during pelagic foraging trips that typically last several days or weeks, 'off-duty' albatrosses need to gain mass rapidly in order to restore body condition and accumulate energy for the next (long) fast at the nest. Birds that do not accumulate sufficient reserves during a foraging trip risk failing to complete the following incubation shift; on the other hand, birds that remain at sea for too long risk returning to a nest already deserted by the incubating partner (Weimerskirch 1995). Hence, during incubation, foraging albatrosses have a considerable incentive to gain mass at a maximum rate, while keeping foraging trips relatively short. Foraging trip duration and daily mass gain are therefore two highly relevant parameters reflecting the foraging performance of individuals.

Using one of the few long-term study populations of a very long-lived bird, we measured foraging trip duration and daily mass gain of individual grey-headed albatrosses of different ages. We also contrasted hatching and breeding success of pairs composed of two old individuals, with those of mid-aged birds. Furthermore, we compared past reproductive effort of the birds under observation, to evaluate the possibility that our results were confounded by demographic heterogeneity and phenotypic correlations between reproduction and survival. Our analyses focused on individuals that were known to have survived at least 1 year beyond the field measurements described in this paper, hence avoiding studying birds that possibly were suffering from an advanced terminal illness.

2. MATERIAL AND METHODS

This study took place at a grey-headed albatross colony (colony E) on Bird Island, South Georgia (54°00′ S, 38°03′ W), in the 2002/2003 breeding season. Chicks in this colony were first ringed in 1958, and since 1975 it has been the subject of an intensive long-term study involving ringing of all nesting adults and monitoring of their survival and reproductive success on an annual basis (Prince *et al.* 1994). All nests in the colony were marked with numbered tags, and laying and hatching dates determined from daily visits. Eggs were measured with callipers. Chick survival to fledging was assessed by weekly visits. Adult birds were sexed on the basis of observations of copulation, pre-laying attendance patterns or molecular techniques.

At the start of the season, all nesting birds in the colony were identified and two groups targeted for the detailed study of body-mass gain. Grey-headed albatrosses first breed when they are 10–14 years old (Prince *et al.* 1994). In this paper, we designated as mid-aged birds all individuals with considerable previous breeding experience (at least four recorded breeding attempts), but not older than 28 years. Old birds included

those, ringed as chicks, that were known to be at least 39 years old, and those that had bred first in 1978 or earlier and hence could be assumed to be at least 35 years old. The oldest four known-age birds in our sample were 44 years old in 2002/2003, but others (e.g. all those ringed as adults from 1958 to 1964) would have been even older. These groups were defined before data collection took place, i.e. cut-off points were chosen *a priori*. Body-mass measurements were only taken from birds in the two pre-defined groups.

Foraging trip duration was determined from a daily visit to each nest to identify the incubating bird. Foraging trips in mid-incubation by satellite-tagged birds lasted a minimum of 7 days, and it is unlikely that others by marked birds could have lasted less than 24 h and been missed. When present at the colony (incubating), each target study bird was weighed every 48 h using a Pesola balance, according to the technique described by Prince *et al.* (1981). Birds were not restrained in any way, and disturbance was therefore kept to a minimum. Despite these efforts, it is possible that our presence elicited physiological responses such as increased heart rate and body temperature (e.g. Regel & Pütz 1997). However, such effects were probably mild (disturbance was low compared to other behavioural and ecological studies of seabirds), and there is no reason to believe that they would have differentially affected birds of various age groups.

Body mass at arrival was considered to be that measured on the first day seen at the colony after a foraging trip. Body mass at departure was the mass measured on the last day before departure. When either was unavailable, mass was predicted from an equation relating mass change to time since the start of the incubation shift (Prince *et al.* 1981). Individual equations were fitted for each bird based on the mass recorded every 48 h during a particular incubation shift. Mass gain during the trip is the difference between mass at departure and mass at arrival, and daily mass gain is the overall mass gain divided by the number of days that the bird was at sea. To reduce, as far as possible, other sources of variability (e.g. variation in behaviour associated with proximity to the date of hatching), we only considered data relating to the second foraging trip of each individual during incubation. This approach also eliminated potential pseudo-replication in statistical analyses. Because of time constraints, some individuals were not weighed regularly, although their nest attendance was still monitored; this explains the differences in sample sizes between analyses of trip duration and mass gain.

At the end of incubation, adults were measured (bill length, bill depth and wing length). These data were incorporated in a principal component analysis, and score in the first principal component (PC1—corresponding to a body-size index; Rising & Somers 1989) was incorporated as a covariate in the analyses of daily mass gain.

When comparing breeding performance of different age classes, we only included data from pairs where both individuals belonged to the same age class. Fledging success is the percentage of hatched chicks in each group that fledged, and breeding success is the percentage of eggs laid that produced a fledgling. To identify birds surviving at least 1 year beyond our measurements of foraging and breeding performance, the study colony was visited daily during egg-laying in the 2003/2004, 2004/2005 and 2005/2006 breeding seasons, and the identities of all birds recorded.

To evaluate whether old- and mid-aged individuals differed in past reproductive effort, we used data from the eight breeding seasons prior to 2002/2003. We reasoned that, in albatrosses, breeding failures generally occur up to the middle of the breeding cycle. Hence, a successful breeding attempt probably implies at least twice as much reproductive effort as an unsuccessful one. Hence, in our analyses, a failed breeding attempt was scored as one unit of past reproductive effort, while a successful attempt represented two units. Analysing past reproductive effort as the number of breeding attempts, without taking into account successes and failures, yielded essentially the same results (not presented in this paper).

3. RESULTS

(a) *Foraging performance*

Foraging trips (the second foraging trip of each bird during incubation) lasted 14.7 ± 3.5 days (range: 8–28 days; $n = 99$), with an average mass gain of 610 ± 230 g per trip (range: 140–1550 g; $n = 86$), equating to a mean rate of 44 ± 18 g per day (range: 10–103 g; $n = 86$). Foraging trip duration was repeatable, as shown by a positive correlation between the duration of the first and second incubation foraging trips of the same individuals ($r = 0.48$, $n = 48$, $p = 0.001$). We have no data to perform a similar test in relation to mass gain, because masses were only taken both before and after the second foraging trip.

We studied the effect of age group on foraging trip duration and daily mass gain separately for males and females, because preliminary analyses indicated the existence of significant interactions between age and sex, and because we know that male and female grey-headed albatrosses from this colony have different foraging strategies and foraging domains (Phillips *et al.* 2004).

Among males that survived at least 1 year beyond these measurements, the second foraging trip duration was 28% longer in old birds, and the daily mass gain was 65% higher in mid-aged individuals (figures 1 and 2). Among females, there were no significant differences between mid-aged and old individuals (figures 1 and 2). Inclusion of duration of the previous incubation stint or body mass at departure as covariates in the general linear models did not change these results, suggesting that the behaviour of the partner did not influence that of the focal study birds. The same was true when PC1 score was included as a covariate in the analyses of daily mass gain, to account for possible confounding effects of body size.

The differences between mid-aged and old-aged males remained if analyses were repeated only using data from individuals known to have survived 2 years beyond field measurements, but with this reduced sample size, only the effect of age on foraging trip duration remains statistically significant at $p < 0.05$ (table 1). There were no differences in past reproductive effort between mid-aged (5.7 ± 1.2 'units of effort', $n = 52$) and old individuals (5.7 ± 1.3, $n = 52$; $F = 0.006$, $p = 0.94$). Incorporating this variable as a covariate in the analyses of the influence of age on trip duration and on daily mass gain did not change the results presented in figures 1 and 2.

(b) *Breeding performance*

Considering only pairs in which both partners were known to have survived at least one further year, hatching success of old pairs ($8/13 = 62\%$) was significantly lower than that of mid-aged pairs ($16/16 = 100\%$, Fisher's exact test,

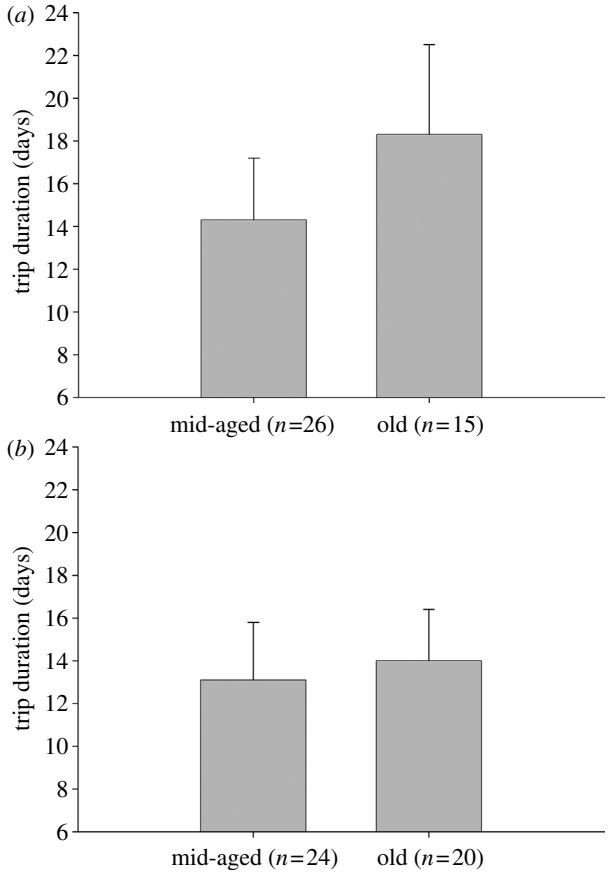

Figure 1. Differences between mid-aged and old grey-headed albatrosses in foraging trip duration of (*a*) males ($F_{1,39}=12.9$, $p=0.001$) and (*b*) females ($F_{1,42}=1.4$, $p=0.25$). Only birds that survived at least 1 year beyond these measurements are included.

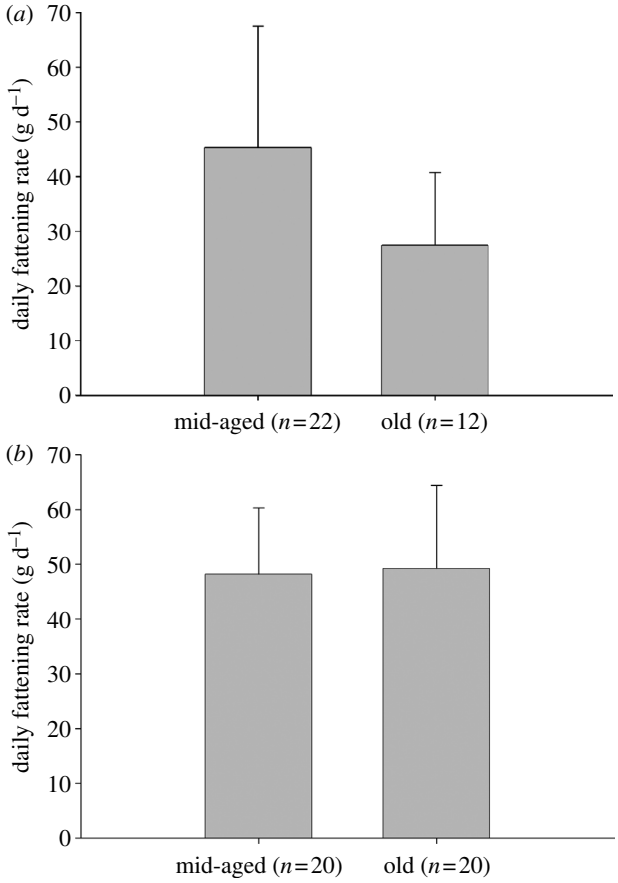

Figure 2. Differences between mid-aged and old grey-headed albatrosses in daily mass gain of (*a*) males ($F_{1,32}=6.4$, $p=0.016$) and (*b*) females ($F_{1,38}=0.14$, $p=0.72$). Only birds that survived at least 1 year beyond these measurements are included.

$p=0.01$). Overall breeding success of old pairs (2/13=15%) was around one-third that of mid-aged pairs (7/16=44%), but the sample size is small and the difference falls short of significant (Fisher's exact test, $p=0.13$). Note that when we include all pairs studied, irrespective of their posterior fate, the differences are significant: old pairs had lower breeding success (3/19=16%) than pairs composed of two mid-aged individuals (13/23=57%; Fisher's exact test, $p=0.01$). There were no differences in mean laying date ($F_{1,27}=0.27$, $p=0.61$) or egg volume ($F_{1,27}=0.30$, $p=0.59$) between age classes. Too few chicks survived long enough to make meaningful comparisons of chick growth between groups.

The sum of past reproductive effort of individuals in partnerships of old birds (11.1±2.7 units of effort, $n=19$) was not significantly inferior to the value obtained for mid-aged partnerships (11.8±2.5 units of effort, $n=16$; $F=0.64$, $p=0.43$).

4. DISCUSSION

The ideas and evidence presented recently by Ricklefs (2000) and Coulson & Fairweather (2001) suggest that birds can maintain high levels of physical fitness until old age. This is very different from humans, for whom reduced physical fitness with aging is obvious, and several other species of mammal, in which aging apparently increases vulnerability to extrinsic causes of death (Ricklefs & Scheuerlein 2001). Previous studies apparently documenting progressive declines in breeding performance of senescent birds are potentially inconclusive because of the inevitable inclusion of some terminally ill individuals in cross-sectional analyses. Our study was specifically designed to deal with this and other major potential problems. By studying an extremely long-lived species, in which many individuals are expected to reach ages where senescence effects might occur (Ricklefs 2000), we were able to demonstrate a clear decline in foraging and breeding performance in old individuals and pairs.

Many studies have recorded apparent improvements in foraging ability with age in young birds (Wunderle 1991), but, to our knowledge, this is the first report of a decline in foraging performance with old age (but see Galbraith *et al.* 1999). Documenting such a reduction in foraging performance is critical, given that this factor is likely to affect all fitness correlates in senescent individuals, including the capacity to attend and defend a nesting site, attract a partner, care for offspring and survive to the following breeding season. This reduced foraging performance might provide a link between reproductive and actuarial senescence.

That we identified an age-related reduction in foraging performance in old males, but not females, is not necessarily indicative of fundamental variation in the pattern of senescence in the two sexes (although such a difference might exist). As in other albatrosses (e.g. Weimerskirch 1995), male and female grey-headed albatrosses have different foraging domains during the

Table 1. Mean foraging trip duration and daily mass gain of mid-aged and old male grey-headed albatrosses. (Only individuals known to have survived at least 2 years beyond the field measurements were included in these statistics.)

	mid-aged birds (*n*)	old birds (*n*)	statistical comparison
trip duration (days)	14.5±3.0 (21)	16.8±3.1 (11)	$F=4.2$, $p=0.048$
daily mass gain (g d^{-1})	43.6±23.3 (17)	28.6±14.3 (9)	$F=3.1$, $p=0.09$

incubation phase, with satellite-tracked females feeding much closer to South Georgia than males (Phillips *et al.* 2004), hence the shorter female trips reported here. In our study, males had lower rates of daily mass gain than females, suggesting that feeding conditions were comparatively unfavourable in the more distant areas. Differences between age groups in performance might only be apparent when conditions are well below optimal (Sydeman *et al.* 1991), which could be the reason why only males showed such a pattern here. In any case, the broader study of breeding success in relation to age confirmed that pairs of old birds had a low reproductive output, irrespective of the contribution of males and females.

Moreover, our analyses relating to foraging performance are possibly somewhat conservative. If old individuals defer nesting more often because of senescence effects (Weimerskirch 1992; Catry *et al.* 1998), then our sample of old birds might be more biased towards fit individuals than the sample of mid-aged ones. In addition, some birds (mostly old) had already failed before their foraging performance could be measured, which again might mean that only relatively fit individuals were available for our study.

Life-history theory predicts that old birds, because of their reduced residual reproductive value, should invest more in the current breeding attempt at the expense of future reproduction (Stearns 1992). This prediction has not generally been upheld by empirical analyses in long-term studies (e.g. Reid 1988; Forslund & Pärt 1995, but see Pärt *et al.* 1992). This failure could be explained if general physical condition has already deteriorated in individuals old enough to have relatively low prospects of breeding successfully in the future. Reduced physical fitness might therefore mask the effect of any increases in reproductive effort, in relation to breeding output.

Mid-aged and old individuals included in this study did not, on average, differ in past reproductive effort, and the inclusion of this variable as a covariate in our analyses did not change the overall results. Hence, a negative phenotypic covariance between traits that favour reproduction and survival, which can potentially affect any cross-sectional analysis (Pugesek & Wood 1992; Nisbet 2001), is not evident in this species and is most unlikely to represent a confounding factor in our study.

Non-adaptive philopatry to deteriorating nest sites is unlikely to have contributed to the poor performance of old pairs. Nests of grey-headed albatrosses on Bird Island are partly or entirely rebuilt every year. Also, birds often are forced to move to new sites as a consequence of failed individuals from the previous season returning to try to breed at exactly the same site as successful birds from two seasons before. Because grey-headed albatrosses are extremely long-lived and nests short-lived, it is most unlikely that old individuals, on average, use older nests than mid-aged individuals. Non-adaptive philopatry to nest sites obviously cannot explain age-related differences when foraging away from the breeding colony, such as the ones documented here.

On the basis of their comparative analyses of actuarial senescence, Ricklefs & Scheuerlein (2001) suggested that increased mortality in old age results largely from catastrophic death from intrinsic causes. They regarded 'catastrophic' to be 'death that occurs relatively quickly without a prolonged debilitating illness that would increase vulnerability to extrinsic factors' (p. 855). The implication is that birds retain a high level of physical fitness until old age. Our results, however, suggest that in grey-headed albatrosses there is a decline in foraging performance at least 2 years before death, i.e. well before the terminal breeding attempt. This accords with a recent study of the shorter-lived common gull *Larus canus*, indicating that even when only considering the penultimate breeding attempt (hence all individuals survived at least another year), old birds had a reduced probability of producing a recruit (Rattiste 2004).

Our study also highlights, contrary to the terminal illness hypothesis (Coulson & Fairweather 2001), that long-lived birds can show signs of depressed physical condition well before the terminal breeding attempt. The possibility remains, however, that extremely long-lived birds could survive for several years while suffering from a terminal illness. Such a hypothesis would be extraordinarily difficult to test, given the requirement to assess by detailed veterinary exam whether or not most individuals showing a decline in reproductive or other function are suffering from a slowly developing irreversible illness that will eventually lead to their demise. However, it seems hard to imagine a scenario where a large proportion of the terminal illnesses affecting a population would significantly impair the physical performance of non-senescent individuals at least 2 years before their death.

In conclusion, our study demonstrates for the first time that long-lived birds can display a senescence-related decline in reproductive function and in foraging performance years before their death. More research is needed to evaluate whether such a decline only occurs in the presence of a slowly developing terminal illness, or if apparently healthy individuals suffer from a progressive general wear and tear such as that afflicting mammals, including humans.

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REFERENCES

Bradley, J. S., Wooller, R. D., Skira, I. J. & Serventy, D. L. 1990 The influence of mate retention and divorce upon reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *J. Anim. Ecol.* **59**, 487–496.

Catry, P., Ratcliffe, N. & Furness, R. W. 1997 Partnerships and mechanisms of divorce in the great skua *Catharacta skua*. *Anim. Behav.* **54**, 1475–1482. (doi:10.1006/anbe.1997.0552)

Catry, P., Phillips, R. A., Hamer, K. C., Ratcliffe, N. & Furness, R. W. 1998 The incidence of non-breeding by adult great skuas and parasitic jaegers from Foula, Shetland. *Condor* **100**, 448–455.

Coulson, J. C. & Fairweather, J. A. 2001 Reduced reproductive performance prior to death in the Black-legged Kittiwake: senescence or terminal illness? *J. Avian Biol.* **32**, 146–152. (doi:10.1034/j.1600-048X.2001.320207.x)

Finch, C. E. & Austad, S. N. 2001 History and prospects: symposium on organisms with slow ageing. *Exp. Gerontol.* **36**, 593–597. (doi:10.1016/S0531-5565(00)00228-X)

Forslund, P. & Pärt, T. 1995 Age and reproduction in birds. Hypotheses and tests. *Trends Ecol. Evol.* **10**, 374–378. (doi:10.1016/S0169-5347(00)89141-7)

Galbraith, H., Hatch, J. J., Nisbet, I. C. T. & Kunz, T. H. 1999 Age-related changes in efficiency among breeding common terns *Sterna hirundo*: measurements of energy expenditure using double-labelled water. *J. Avian Biol.* **30**, 85–96.

Holmes, D. J. & Austad, S. N. 1995 The evolution of avian senescence patterns: implications for understanding primary aging processes. *Am. Zool.* **35**, 307–317.

Holmes, D. J., Flückiger, R. & Austad, S. N. 2001 Comparative biology of aging in birds: an update. *Exp. Gerontol.* **36**, 869–883. (doi:10.1016/S0531-5565(00)00247-3)

Newton, I. (ed.) 1989 *Lifetime reproduction in birds*. London, UK: Academic Press.

Newton, I. & Rothery, P. 1997 Senescence and reproductive value in sparrowhawks. *Ecology* **78**, 1000–1008.

Nisbet, I. C. T. 2001 Detecting and measuring senescence in wild birds: experience with long-lived seabirds. *Exp. Gerontol.* **36**, 833–843. (doi:10.1016/S0531-5565(00)00244-8)

Nisbet, I. C. T., Apanius, V. & Friar, M. S. 2002 Breeding performance of very old common terns. *J. Field Ornithol.* **73**, 117–124.

Pärt, T., Gustaffson, L. & Moreno, J. 1992 'Terminal investment' and a sexual conflict in the collared flycatcher (*Ficedula albicollis*). *Am. Nat.* **140**, 868–882. (doi:10.1086/285445)

Phillips, R. A., Silk, J. R. D., Phalan, B., Catry, P. & Croxall, J. P. 2004 Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. R. Soc. B* **271**, 1283–1291. (doi:10.1098/rspb.2004.2718)

Prince, P. A., Ricketts, C. & Thomas, G. 1981 Weight loss in incubating albatrosses and its implications for energy and food requirements. *Condor* **83**, 238–242.

Prince, P. A., Rothery, P., Croxall, J. P. & Wood, A. G. 1994 Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* **436**, 50–71.

Pugesek, B. H. & Wood, P. 1992 Alternate reproductive strategies in the California gull. *Evol. Ecol.* **6**, 279–295. (doi:10.1007/BF02270965)

Rattiste, K. 2004 Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life. *Proc. R. Soc. B* **271**, 2059–2064. (doi:10.1098/rspb.2004.2832)

Regel, J. & Pütz, K. 1997 Effect of human disturbance on body temperature and energy expenditure in penguins. *Polar Biol.* **18**, 246–253. (doi:10.1007/s003000050185)

Reid, W. V. 1988 Age-specific patterns of reproduction in the glaucous-winged gull: increased effort with age. *Ecology* **69**, 1454–1465.

Ricklefs, R. E. 1998 Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *Am. Nat.* **152**, 24–44. (doi:10.1086/286147)

Ricklefs, R. E. 2000 Intrinsic aging-related mortality in birds. *J. Avian Biol.* **31**, 103–111. (doi:10.1034/j.1600-048X.2000.210201.x)

Ricklefs, R. E. & Scheuerlein, A. 2001 Comparison of aging-related mortality among birds and mammals. *Exp. Gerontol.* **36**, 845–857. (doi:10.1016/S0531-5565(00)00245-X)

Rising, J. D. & Somers, K. M. 1989 The measurement of overall body size in birds. *Auk* **106**, 666–674.

Rockwell, R. F., Cooch, E. G., Thompson, C. B. & Cooke, F. 1993 Age and reproductive success in female lesser snow geese: experience, senescence and the cost of philopatry. *J. Anim. Ecol.* **62**, 323–333.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.

Sydeman, W. J., Penniman, J. F., Penniman, T. M., Pyle, P. & Ainley, D. G. 1991 Breeding performance in the western gull: effects of parental age, timing of breeding and year in relation to food availability. *J. Anim. Ecol.* **60**, 135–149.

Weimerskirch, H. 1992 Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in wandering albatross. *Oikos* **64**, 464–473.

Weimerskirch, H. 1995 Regulation of foraging trips and incubation routine in male and female wandering albatross. *Oecologia* **102**, 37–43.

Wunderle Jr, J. M. 1991 Age-specific foraging proficiency in birds. In *Current ornithology*, vol. 8 (ed. D. M. Power), pp. 273–324. New York, NY: Plenum Press.